

1 **Title:** Identifying thresholds of logging intensity on dung beetle communities to improve the  
2 sustainable management of Amazonian tropical forests

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26 **Abstract:** Selective logging is the most widespread driver of tropical forest disturbance. As  
27 such, it is critically important to identify at which spatial scale logging intensity should be  
28 measured and whether there are clear thresholds in the relationship between logging intensity  
29 and its impacts on biodiversity or ecological processes. We address this using a robust before-  
30 and–after logging experimental design in the Brazilian Amazon, using a gradient of logging  
31 intensity measured at two different spatial scales. We assessed the impacts of selective logging  
32 using dung beetle communities and their ecological functions of dung removal and soil  
33 bioturbation. Our findings provide novel empirical evidence that biological consequences from  
34 Reduced Impact Logging (RIL) depend strongly on the scale at which logging intensity is  
35 measured: dung beetle local species richness and composition were strongly associated with  
36 logging intensity measured at a 10ha scale, while dung beetle-mediated soil bioturbation was  
37 more strongly associated with logging intensity measured across 90ha. Contrary to  
38 expectations, we found concave-shaped relationships between logging intensity and  
39 biodiversity and ecosystem functioning, demonstrating that sensitive dung beetle species and  
40 important processes may be lost following even low intensity anthropogenic forest  
41 disturbances. Taken together, these results suggest that production forests in the tropics need to  
42 reconsider the scale at which logging intensity is regulated, and put in place measures that  
43 further incentivise land sparing to enhance biodiversity conservation.

44 **Keywords:** Biodiversity; Brazilian Amazon; threshold; tropical forest; selective logging  
45 intensity; land-sparing.

## 46 **1.1 Introduction**

47 More than 403 million hectares of tropical forests have been officially designated for timber  
48 concessions (Blaser et al., 2011), where selective logging is one of the most widespread  
49 economic activities (Guariguata et al., 2010). Although it is undoubtedly less environmentally  
50 severe than many other human disturbances (Barlow et al., 2006; Gibson et al., 2011), selective  
51 logging remains an important driver of tropical forest degradation (Gatti et al., 2015), reducing  
52 carbon stocks (Berenguer et al., 2014) and negatively affecting both forest biodiversity (Barlow  
53 et al., 2016; Martin et al., 2015) and ecosystem functioning (Griscom et al., 2017; Slade et al.,  
54 2011). Given its spatial extent and economic importance, improvements in the sustainability of  
55 forest management are fundamental for conservation in the tropics (Bicknell et al., 2014b);  
56 sustainable forest management is the most adopted REDD+ intervention in tropical regions  
57 (Salvini et al., 2014) and is enshrined as a key aim of international biodiversity targets for 2020  
58 (Convention on Biological Diversity, 2014).

59 Although the ecological consequences of Reduced Impact Logging (RIL) operations are  
60 well studied, there are three key knowledge gaps which limit the ability of ecological science to  
61 inform policy and management decisions. First, there is no evidence to determine the most  
62 appropriate spatial scale for prescribed limits on logging intensity. For example, Brazilian  
63 Forestry legislation (CONAMA, Resolution no. 1 of 2015) requires Annual Planning Units in  
64 Amazonia to maintain at least 15% of all large trees, or three large trees per 100 ha from each  
65 exploited species, as seed bearers. However, these requirements, including the use of the 100-  
66 ha scale, are not supported by scientific evidence. This lack of information is important as a  
67 growing number of studies on different taxa demonstrate spatial scale-dependent responses of  
68 species richness to logging impacts (Cleary et al., 2009; Imai et al., 2012), and there is also  
69 growing evidence that other biological metrics could respond to forest degradation at different  
70 spatial scales (Martel et al., 2007; Solar et al., 2015).

71           The second key limitation relates to the shape of the biological responses to logging  
72 intensity. Recent meta-analysis studies have demonstrated that logging impacts on forest  
73 structure and biodiversity are proportional to logging intensity (Burivalova et al., 2014; Martin  
74 et al., 2015). They also highlight the possibility of non-linear biological responses, suggesting  
75 there may be thresholds in logging intensity above which animal species richness decreases  
76 (Burivalova et al., 2014). Defined as change points or zones at which sudden regime shifts  
77 occur from one ecological condition to another, ecological thresholds are likely if disturbance  
78 intensity induces non-linear effects on community structure, composition and ecological  
79 functioning (Huggett, 2005). Identifying these thresholds is therefore a major challenge for  
80 improving the sustainability of forest management (DeFries et al., 2004), and depending on the  
81 shape of the biodiversity response (Fig. 1), could even help inform decisions about the land-  
82 sparing vs. land-sharing logging management debate (Edwards et al., 2014a; Law and Wilson,  
83 2015; Phalan et al., 2011). Yet, no study has identified any such threshold with selective  
84 logging (Burivalova et al., 2014).

85           Finally, despite progress made in our understanding of the logging impacts on species  
86 composition and ecosystem functions (Ewers et al., 2015; Imai et al., 2012), the majority of  
87 these investigations treat selective logging as a uniform disturbance with mean effect size. As a  
88 result, we still lack empirical evidence outlining how multiple metrics of ecological integrity,  
89 including species composition and ecological functioning, respond along gradients of selective  
90 logging intensity.

91           We address the above knowledge gaps using a robust Before-After-Control-Impact  
92 (BACI) experimental design in the eastern Brazilian Amazon to assess how logging intensity,  
93 and the spatial scale at it is measured, affects dung beetle species richness, biomass, species  
94 composition, and their associated ecological functions of dung removal and soil bioturbation.  
95 We focus on dung beetles (Coleoptera: Scarabaeinae) as they are good predictors of responses  
96 of many other taxa (Edwards et al., 2014b; Gardner et al., 2008a) and have been recommended

97 as cost-effective and highly responsive indicators of changes caused by human disturbances in  
98 tropical forests (Bicknell et al., 2014a; França et al., 2016a). We focus on richness and  
99 composition as these metrics have been frequently used to assess changes in  $\alpha$  (local diversity)  
100 and  $\beta$ -diversity (compositional turnover), respectively (Gardner et al., 2008b; Socolar et al.,  
101 2015). We include biomass because it has been frequently used to evaluate the consequences of  
102 tropical forest degradation on dung beetles (França et al., 2016b; Griffiths et al., 2016b) and is  
103 a key trait influencing dung beetle-mediated ecological functions (Gregory et al., 2015;  
104 Griffiths et al., 2016a). Finally, we measure the dung burial and soil bioturbation functions  
105 (Nichols et al., 2008), which provide insights into how dung beetles may modify the soil  
106 microflora (Slade et al., 2016b), enhance the plant growth (Griffiths et al., 2016a; Yamada et  
107 al., 2007), and even reduce greenhouse gas emissions (Slade et al., 2016a).

108 We explore two hypotheses. First, while management decisions limiting timber  
109 extraction are made on a 100-ha scale, we predict that smaller scale (10 ha) measurements of  
110 logging intensity will better predict responses of dung beetle community metrics and  
111 ecological functions. This is because logging intensity varies more when measured at smaller  
112 scales (large scales tend to converge to landscape averages) and because dung beetles are  
113 known to be sensitive to local changes in forest structure and microclimate following  
114 disturbance (Mehrabi et al., 2014; Silva and Hernández, 2016). Second, we use the spatial scale  
115 identified as the strongest predictor in the first hypothesis to examine the shape of the  
116 responses of dung beetle metrics to gradients of selective logging intensity. We predict that  
117 these relationships will be better explained by threshold-like models that are concave in shape  
118 rather than linear ones. We make this prediction because (a) concave-shaped threshold  
119 relationships have been found in land-use change studies assessing the relationships between  
120 forest cover and estimates of species richness based on multiple taxa (Muylaert et al., 2016;  
121 Ochoa-Quintero et al., 2015), and because (b) dung beetle diversity and ecological functions  
122 are known to decrease in highly disturbed forests (Braga et al., 2013), but can be maintained in

123 low-intensity logged forests (Slade et al., 2011) or even after repeated logging rotations  
124 (Edwards et al., 2014).

## 125 **2. Methods**

### 126 *2.1 Study area*

127 The study was based within the 1.7-Mha *Jari Florestal* logging concession located at the State  
128 of Pará in the north-eastern Brazilian Amazon (0°27'S 51°40'W; appendix A, Fig. A.1). The  
129 region comprises a mosaic of regenerating native vegetation and *Eucalyptus* plantations  
130 embedded within a large matrix of virtually undisturbed primary forests (Barlow et al., 2010;  
131 Gardner et al., 2008b).

132 This RIL concession covers about 544,000 ha of native forest, and the logging plan  
133 follows the FAO model code over a 30-year cutting cycle (Dykstra and Heinrich, 1996).  
134 During the pre-harvest inventory the logging concession is subdivided into 10 ha (250 x 400  
135 m) planning units where commercially viable trees with d.b.h  $\geq$  45cm are mapped, identified  
136 and measured to provide the basis for planning the logging. The harvesting and extraction of  
137 timber along skid trails take place during the dry season (August to November), one year after  
138 the planning inventory. RIL is supported by using directional felling to minimise incidental  
139 damage to other trees, and cutting lianas on large trees during the inventory stage (Putz et al.,  
140 2008).

### 141 *2.2 Experimental design*

142 We used the company's pre-harvest operational plan to select 34 sites (hereafter sample units)  
143 in the timber concession. These included five control sites that would not be logged during the  
144 course of the study, and 29 logging units which were destined to be logged between July and  
145 September 2012. As we aimed to assess the logging impacts as a continuous (rather than  
146 categorical) effect, sample units were selected along a gradient of planned logging intensities,  
147 which resulted in 0 - 50.3 m<sup>3</sup> ha<sup>-1</sup> of timber (or 0 - 7.9 trees ha<sup>-1</sup>) that was eventually extracted.

148 The five unlogged control units included in this range were the same size (250 m ×400 m; 10  
149 ha) as the logged units, and were located approximately 6.5 km from the closest logged units to  
150 avoid any spillover effects from logging operations (Block et al., 2001). Importantly, these  
151 control units held a dung beetle community representative of the undisturbed primary forests in  
152 our study region (França et al., 2016b).

153 After logging operations in 2012, the planned harvest intensities within each sampled  
154 unit were fulfilled, resulting in an average timber removal of  $\sim 16.8 \text{ m}^3 \text{ ha}^{-1}$  across this logging  
155 concession. Therefore, we assumed the volume of removed timber per hectare (measured as the  
156 sum of the volume of timber logs extracted from each removed tree) as our measure of logging  
157 intensity and explanatory variable for all analyses, as this has been previously applied to assess  
158 logging intensity thresholds for biodiversity (Burivalova et al., 2014; Martin et al., 2015).  
159 Moreover, like others (Picard et al., 2012), we found high co-linearity among volume of  
160 removed timber and number of logged trees ( $N = 34$ ,  $R^2 = 0.91$ ,  $p < 0.001$ ; appendix A, Fig.  
161 A.2).

162 We sampled dung beetles and their ecological functions twice (pre and post-logging) in  
163 all 34 sample units. The pre-logging survey occurred between June and July 2012,  
164 approximately 45 days before the start of logging operations. The post-logging survey took  
165 place in the same months (June and July) in 2013, approximately 10 months after logging  
166 activities ended. Post-logging dung beetles and ecological functions were always sampled in  
167 exactly the same locations, and followed the same methods used in the pre-logging survey  
168 (França et al., 2016b).

### 169 *2.3 Dung beetles community functions*

170 We evaluated the ecological functions of soil bioturbation and dung removal performed by the  
171 dung beetles following the protocol proposed by Braga *et al.* (2013), setting up two arenas per  
172 sampled unit (appendix A, Fig. A.3a). Each arena was a circular plot of  $\sim 1 \text{ m}$  in diameter and  
173 area of  $\sim 0.79 \text{ m}^2$ , delimited by a nylon net fence (15 cm high) held by bamboo sticks, which

174 limited the horizontal movement of dung by the beetles to the contained area, allowing a more  
175 accurate quantification of the examined functions (Appendix A, Fig. A.4a). We also cleared the  
176 soil surface of any leaf litter and vegetation before placing each arena to facilitate the  
177 measurement of ecological functions (Braga et al., 2013). In the centre of each arena we placed  
178 a 200-g dung pile (4:1 pig to human ratio, following Marsh *et al.* 2013), which was protected  
179 from the rain by a plastic lid and exposed in the field for 24 h. This exposure period was  
180 chosen based on known movements of dung beetles (Silva and Hernández, 2015) and to reduce  
181 the risk of beetles from outside the sample unit perform the ecological functions within the  
182 arenas. After 24 h, the remaining dung (when present) was collected, taken to the laboratory  
183 and weighed to quantify dung removal. We set a parallel humidity control experiment,  
184 excluding all insect groups from the dung, to account for water loss or gain in the calculation  
185 of dung removal (see appendix A, Fig. A.4b and appendix B, for details of the humidity control  
186 experiment). Therefore, to quantify the ecological function of soil bioturbation as a  
187 consequence of tunnel building by the dung beetles, we collected the loose soil clearly found  
188 above the soil surface with spoons and spatulas, and weighed it after drying at 60 °C for a week  
189 (Braga et al., 2013). In both pre and post-logging surveys, measures of dung removal and soil  
190 bioturbation from the two arenas were pooled to get an aggregate value for each sample unit.

#### 191 *2.4 Dung beetle surveys*

192 Dung beetles were sampled using six pitfall traps spaced 100 m apart in a 2x3 m rectangular  
193 grid, so that traps were at least 75 m from the edge of the unit (see appendix A, Fig. A.3b).  
194 This spacing of traps helped ensure an even spatial coverage of each sample unit. Pitfalls (19  
195 cm width, 11 cm depth) were buried flush with the ground, containing ~250 ml of a saline  
196 solution, and baited with *c.* 35 g of fresh pig dung mixed with human dung (4:1 pig to human  
197 ratio, following Marsh *et al.* 2013). In both survey periods, all pitfalls were placed immediately  
198 after withdrawal of the ecological function arenas, and data from the six pitfalls in each unit

199 were pooled to get an aggregate value and improve representation of dung beetle metrics  
200 within each sample unit.

201 We restricted our sample window to 24 hours in each survey period, as short sample  
202 periods are known to be efficient at attracting a representative sample of the local beetle  
203 community (Braga et al., 2013; Estrada and Coates-Estrada, 2002) and 24 hours is a good  
204 predictor of community metrics from longer sampling durations (França et al., 2016b). Longer  
205 sample periods were not chosen as they would increase the probability of attracting dung  
206 beetles from outside the sample units (Silva and Hernández, 2015), and therefore from units  
207 with different logging intensities. All trapped dung beetles were processed in a laboratory  
208 where they were identified to species, or morphospecies where the former was not possible.  
209 We calculated the average biomass of each species from the dry weight of a sample of between  
210 1 and 15 individuals using a *Shimadzu AY220* balance (*Shimadzu Corporation, Kyoto, Japan*)  
211 with precision to 0.0001g. Sampling did not involve any endangered species and permission to  
212 collect zoological material was granted by the *Instituto Chico Mendes de Conservação da*  
213 *Biodiversidade* (ICMBio) prior to the field campaigns of the project (SISBIO nº1620-3/10068).

## 214 2.5 Statistical analyses

215 We ran all statistical analyses in R v. 3.2.0 (R Core Team, 2017). As the BACI approach has  
216 been suggested to better evaluate biodiversity responses to environmental changes in tropical  
217 forests (França et al., 2016b), we considered the pre-logging data as a baseline for post-logging  
218 dung beetle community metrics and ecological functions. Thus, we used  $\Delta$  species richness,  $\Delta$   
219 biomass,  $\Delta$  species composition,  $\Delta$  soil bioturbation and  $\Delta$  dung removal as response variables.  
220  $\Delta$  was based on the difference between total species richness, biomass, and rates of soil  
221 bioturbation and dung removal from post-logging minus pre-logging survey within each  
222 sampled unit. The  $\Delta$  species composition, considered as the pairwise beta-diversity (Socolar et  
223 al., 2015), was calculated through the *vegdist* function in *vegan* (Oksanen et al., 2015) based on

224 the Bray–Curtis similarity index (1 – dissimilarity) among pre- and post-logging surveys  
225 within each sample unit.

226 Our first hypothesis was that small-scale measurements of logging intensity better  
227 predict dung beetle responses. To test this, we change the extent over which the volume of  
228 removed timber is measured while holding constant the area at which biological metrics were  
229 sampled. We therefore assessed biological metrics responses to logging intensity measured at  
230 two scales: a ‘local scale’, the 10-ha sample unit on which biological metrics were sampled;  
231 and ‘broader scale’, the average logging intensity in the sample units and the eight surrounding  
232 units (totalling 90 ha when all combined, which reflects the 100-ha spatial scale used by  
233 Brazilian law; CONAMA, Resolution no. 1 of 2015). Since the harvest intensity at local and  
234 broader scales are collinear (appendix A, Fig. A.2), we analyse these spatial scales separately.  
235 We modified the function from Nagai (2011) and used the Akaike’s criteria for small samples  
236 (AICc) to identify the spatial scale of logging intensity that is the strongest predictor of each  
237 dependent variable. Because models with lower AICc display lower information loss and  
238 express the highest model likelihood (Burnham et al., 2011), we compared AICc weights from  
239 best broader scale models (linear or broken stick regressions) with those obtained from local  
240 scale. Models with the lowest AICc values were accepted as the best fit when the AICc  
241 difference between models was  $> 2$ .

242 Our second hypothesis was that threshold-like models, rather than linear regressions,  
243 would better explain the relationships between beetle metrics and logging intensity. As before,  
244 we used a model-comparison function to determine the most suitable models through the AICc  
245 comparisons between linear and broken-stick models from the same dataset. In cases where the  
246 broken-stick models had the best fit, the breakpoint was estimated. After model selection, we  
247 inspected the residual distribution from all the most suitable models. Finally, we generated the  
248 95% confidence intervals (CI) from the regression lines and, when present, the breaking points  
249 by using the functions *boot.ci* and *confint* from the packages *boot* and *stats*, respectively. Data

250 and R codes used to generate and compare models are available with this paper at the  
251 [Mendeley data repository](#) and Appendix C, respectively.

252 As closer sites may naturally have more closely related biological communities than  
253 those further apart (Soininen et al., 2007), we checked for spatial autocorrelation by performing  
254 Pearson-based Mantel tests with 1000 permutations in the *mantel* function from *vegan*  
255 (Oksanen et al., 2015). We repeated Mantel tests using both the pre- and post-logging dung  
256 beetle species richness, biomass and species composition data, allowing us to examine whether  
257 spatial autocorrelation existed in both sets of analysis. Lastly, we plotted the residuals from the  
258 best models (in terms of scale and regression comparison) on spatial maps of the sample sites,  
259 providing an intuitive visual examination of the presence of any spatial influence in the  
260 analysis (Baddeley et al., 2005; Kühn and Dormann, 2012) (see appendix B, for details of  
261 Mantel tests and residual plots).

### 262 3. Results

263 We recorded 4846 dung beetles in total (3720 and 1126 pre- and post-logging, respectively)  
264 from 53 species (49 pre-logging, 40 post-logging) across our 34 sampled units (see [Mendeley](#)  
265 [repository data](#) for details). Mantel tests of distance between sampled units showed weak but  
266 significant effects of spatial autocorrelation on pre-logging species richness, species  
267 composition and biomass ( $R^2 = 0.18$ ;  $p = 0.005$ ,  $R^2 = 0.35$ ;  $p = 0.001$ , and  $R^2 = 0.12$ ;  $p = 0.03$ ,  
268 respectively). However, the spatial autocorrelation disappeared in the post logging survey for  
269 species richness and biomass ( $R^2 = -0.41$ ;  $p = 0.99$  and  $R^2 = -0.42$ ;  $p = 0.99$ , respectively) and  
270 was greatly reduced for species composition ( $R^2 = 0.18$ ;  $p = 0.01$ ). Finally, there was no  
271 discernible visual association between residuals from best models and geographical location of  
272 sampled sites (see appendix A, Fig. A.5).

#### 273 3.1 Evaluating spatial scales of logging intensity assessment

274 Our first hypothesis, that logging intensity measured at a more local scale would be a better  
275 predictor compared with the broader scale, was supported for the metrics of species richness  
276 and species composition, and a marginally, albeit insignificant, predictor of dung beetle  
277 biomass (see table 1 for AICc values and Residual Sum of Squares). However, logging  
278 intensity at the broader scale was a stronger predictor of the responses of dung beetle-mediated  
279 soil bioturbation (Table 1).

### 280 *3.2 Identifying thresholds in dung beetle responses to selective logging*

281 As expected, dung beetle species richness and composition, biomass, and the ecological  
282 function soil bioturbation were negatively affected by increasing logging intensity (Fig. 2),  
283 although changes in dung removal rates were non-significant. In addition, all beetle community  
284 metrics had significant non-linear relationships with logging intensity (Fig. 2a-c). However,  
285 contrary to our prediction, these non-linear relationships were convex, suggesting a rapid  
286 reduction in biodiversity up to a logging intensity of around 18-20 m<sup>3</sup> ha<sup>-1</sup>, after which there  
287 was no clear additional response to logging intensity (Fig. 2a-c). There was no clear support for  
288 thresholds in the relationship between logging intensity and dung beetle-mediated ecosystem  
289 functions, as the linear and broken-stick models were both plausible predictors of change in  
290 soil bioturbation with logging intensity measured at both scales (Fig. 2d; appendix A, Fig.  
291 A.6d).

## 292 **4. Discussion**

293 Our research makes two novel advances to our understanding of disturbance impacts in tropical  
294 forests. First, it provides strong support to the idea that biological consequences from  
295 anthropogenic disturbances are highly dependent on the scale at which disturbance is measured  
296 (Mayor et al., 2015), recommending the establishment of multiple spatial scales for timber  
297 extraction to improve the sustainability of tropical forest management (Imai et al., 2012; Lunn  
298 et al., 2017) and conserve both biodiversity and their ecological functions. Second, we provide

299 the first empirical evidence that biodiversity and its functions may not respond linearly to  
300 selective logging intensity. Contrary to our expectations, we found evidence suggesting  
301 concave-shaped relationships between logging intensity and most of the metrics evaluated in  
302 our study, which rapidly decreased at low intensities until a threshold of logging intensities of  
303 around 18-20 m<sup>3</sup> ha<sup>-1</sup> measured at the local spatial scale. The concave-shape relationships have  
304 important applied implications as they bolster calls for policy incentives encouraging land  
305 sparing as a conservation strategy within managed tropical forests (Edwards et al., 2014a).

#### 306 *4.1 Scale matters: local biological responses depend on scale of logging assessment*

307 Although disturbance is known to act locally (Barlow et al., 2016; Burivalova et al., 2014), the  
308 scale dependence of logging intensity measurement has been largely overlooked in the  
309 literature. Previous research has manipulated either the scale at which diversity metrics are  
310 measured (Hamer and Hill, 2000), or the scales of diversity and logging assessment (plot size)  
311 are manipulated together (Imai et al., 2012). We provide the first study revealing that distinct  
312 metrics of ecological integrity can depend on the spatial scales at which logging intensity is  
313 measured. Aside from dung beetle biomass, which had both local and broader scales of logging  
314 accurately assessing their patterns, our results show that assessing logging intensities at the  
315 local scale better explained the responses of dung beetle species richness and composition, but  
316 measuring logging intensity at a broader scale provides a better estimate of logging impacts on  
317 soil bioturbation. Given the linkages among biodiversity and ecosystem functioning (Bregman  
318 et al., 2015; Griffiths et al., 2015; Hooper et al., 2012), these results demonstrate the  
319 importance of considering both changes in biodiversity and in ecological functions when  
320 setting timber extraction limits. They also suggest that logging intensity limits (number of trees  
321 or m<sup>3</sup> per ha) should also be applied to smaller and more localised scales to include  
322 consideration of species groups such as dung beetles, which are strongly influenced by local  
323 environment and landscape context (Audino et al., 2017).

#### 324 4.2 Thresholds in biological responses to selective logging

325 To our knowledge, our research is the first empirical study that identifies non-linear biological  
326 responses to logging intensity, adding to meta-analyses that show linear declines across  
327 multiple taxa (Burivalova et al., 2014; Martin et al., 2015). In particular, the dung beetle  
328 diversity metrics we assessed declined sharply up to logging intensities of 9-20 m<sup>3</sup> ha<sup>-1</sup>, after  
329 which their responses flattened. These results reinforce that tropical forest dung beetles are  
330 very sensitive to changes in environmental conditions (França et al., 2016a; Griffiths et al.,  
331 2015) and even low-intensity human impacts (Bicknell et al., 2014a), therefore providing  
332 support about the importance of the logging intensity, here measured as the volume of removed  
333 timber, to determine biodiversity levels within production forests (Burivalova et al., 2014).  
334 Although our finding for species composition should be viewed with caution, the spatial  
335 residual plots (appendix A) and the post-logging absence of spatial autocorrelation for species  
336 richness and biomass made us confident that those metrics are reliably driven by logging  
337 effects rather than natural processes of distance-decay (Kühn and Dormann, 2012; Ramage et  
338 al., 2013).

#### 339 4.3 Does functional change reflect biodiversity?

340 Although the broken-stick and linear models were both plausible for soil bioturbation, both  
341 demonstrated the negative impacts of logging operations on this ecological function. We  
342 believe the decrease in soil bioturbation rates may result from the combined effects from  
343 logging impacts on the dung beetle diversity and forest environmental conditions (Griffiths et  
344 al., 2016a, 2015; Slade et al., 2011), as well as due to the loss of larger-body dung beetles  
345 (Gregory et al., 2015), such as observed for the roller species *Dichotomius boreus* (Olivier,  
346 1789) (see appendix A, Fig. A.7). These changes in soil bioturbation likely reflect a suite of  
347 other ecosystem processes mediated by dung beetles, resulting in changes to the transfer of

348 microbe communities across the soil surface (Slade et al., 2016b) and water permeability and  
349 thus plant productivity (Bang et al., 2005; Griffiths et al., 2016a) within logged forests.

350 However, the absence of significant logging impacts on dung removal rates also  
351 suggests that logged forests may retain part of the ecosystem functions and services from  
352 tropical primary forests (Edwards et al., 2014c), even when highly negative impacts are  
353 observed on the biodiversity (Ewers et al., 2015). This indicates functional redundancy, which  
354 may result from other taxa (e.g. ants and termites) becoming more involved in the detrital  
355 consumption in tropical forests (Dangles et al., 2012).

#### 356 *4.4 Implications for Forest Sustainable Management and tropical conservation*

357 Our findings are particularly important for improving environmental regulations on forest  
358 management adequacy in countries such as Brazil, as their natural resources are coming under  
359 increasing pressure from development programs such as the expansion of logging concessions  
360 in National and State Forests established since 2006 (Law 11.284/2006 by the Brazilian Forest  
361 Service) (BFS, 2013). Previous research has estimated that Brazilian Amazon holds around 4.5  
362  $\pm$  1.35 billion m<sup>3</sup> of commercial timber volume with a likely stumpage value of \$15.5 billion  
363 (Merry et al., 2009), and it easy to foresee an increased demand on Amazonian hardwood as  
364 African and Asian timber stocks are exhausted (Richardson and Peres, 2016).

365 Given this context, it is vital that Brazilian legislation maximizes the sustainability of  
366 logging operations, and minimizes their ecological damage. We show that the current Brazilian  
367 forest legislation, which establishes timber extraction limits in 100-ha blocks (CONAMA,  
368 Resolution no. 1/2015), is failing to consider the biological consequences of harvesting  
369 operations at smaller spatial scales. To improve the conservation value of production forests,  
370 there is an urgent need to incorporate the cross-scale impacts of logging operations on tropical  
371 biodiversity and ecosystem functioning in further timber production-related legislation.

372 Perhaps most importantly, the shape of the non-linear responses of biodiversity and their  
373 related functions provides important insights into the land-sharing vs. land-sparing debate  
374 (Law and Wilson, 2015). The literature has shown that when density-disturbance curves have a  
375 concave shape (Fig. 1), overall density levels on a per species basis may be higher if high-  
376 intensity disturbed patches are mixed spatially within large undisturbed landscapes (Edwards et  
377 al., 2014a; Phalan et al., 2011). Therefore, the concave responses of dung beetle diversity to  
378 logging intensity we have found endorses the proposal that land-sparing logging strategies,  
379 coupled with RIL practices, may increase the conservation value within logging concessions  
380 (Edwards et al., 2014a). These results support recent research that show the importance of  
381 anthropogenic disturbance as a driver of biodiversity loss elsewhere in the Amazon (Barlow et  
382 al., 2016), and the high sensitivity of tropical forest biota to even low levels of human  
383 influence (Betts et al. 2017).

#### 384 *4.5 Further research*

385 The high sensitivity of the dung beetle fauna to logging disturbance in tropical forests highlight  
386 some important avenues for further research. First, longer-term assessments would help  
387 elucidate the temporal dimension of these effects, which is essential given that sustainable  
388 forest management involves c. 25-35 year return intervals (Blaser et al., 2011). Our post-  
389 logging sampling was approximately 10 months after the logging activities; since the logging  
390 impacts may persist for years after the logging operations (Osazuwa-Peters et al., 2015), it may  
391 be that the nature of the response and recovery changes too. Second, our study area was located  
392 in a favourable landscape context surrounded by minimally disturbed primary forests.  
393 However, logging operations are planned in these forests in the coming decades, and it will be  
394 important to examine how the spatial scale of logging management, and the presence of large  
395 unlogged-patches, affect the long-term recovery of biodiversity and ecological processes.  
396 Given the need for larger spatial and temporal-scale monitoring of logging-induced biological

397 consequences (Lunn et al., 2017), these assessments should include multi-scale measurements  
398 of both biotic and forestry metrics. Third, although dung beetles are good indicators of logging  
399 and forest disturbance effects in other taxonomic groups (Barlow et al., 2016; Edwards et al.,  
400 2014b; Gardner et al., 2008a), the response shapes of other taxa require assessment. Finally,  
401 exploring how logging intensity affects individual species density/abundance-timber yield  
402 relationships may also bring insights to fully understand whether land-sparing or sharing  
403 approaches to logging is the most appropriate for biological conservation.

## 404 **5. Conclusion**

405 This research aimed to better understand the impacts of selective logging on biodiversity and  
406 ecological functions, through assessing dung beetle responses along a gradient of logging  
407 intensities measured at two spatial scales. As we provide field evidence that ecological  
408 consequences from harvest operations depend on the scale at which logging intensity is  
409 measured, we highlight that policy makers and researchers should consider the cross-scale  
410 impacts of timber exploration when establishing policy regulations and guidelines related to  
411 sustainable forest management (Imai et al., 2012; Mayor et al., 2015).

412 Our analyses present novel experimental evidence suggesting that biodiversity may  
413 respond non-linearly along a gradient of logging intensity. Surprisingly, the relationships  
414 between most dung beetle metrics and logging intensity were concave in shape, with logging  
415 thresholds around 18-20 m<sup>3</sup> of removed timber. Such logging thresholds can be an important  
416 tool to help tropical forest managers to promote biodiversity conservation within production  
417 forests, while the concave-shaped relationships between logging intensity and dung beetle  
418 responses promote the land-sparing strategy as a conservation priority within tropical logging  
419 concessions (Edwards et al., 2014a). Although we provide support for the assertion that  
420 primary forests are irreplaceable for maintaining tropical biodiversity (Gibson et al., 2011), our  
421 research also reinforces that logged forests have a conservation value in retaining part of the  
422 ecosystem processes from primary forests (Ewers et al., 2015), such as processes related to

423 dung consumption. Finally, we stress the importance of using evidence-based decisions to  
424 minimize the negative impacts of timber production on tropical forest biota and ecological  
425 processes.

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677 **Tables**

678 **Table 1.** Best-fit models ( $AICc \leq 2$ ; in bold) for explaining the relationship between dung  
 679 beetle community metrics and associated ecological functions with the logging intensity  
 680 measured at local (10ha) and broader (90ha) spatial scales in the eastern Brazilian Amazon.

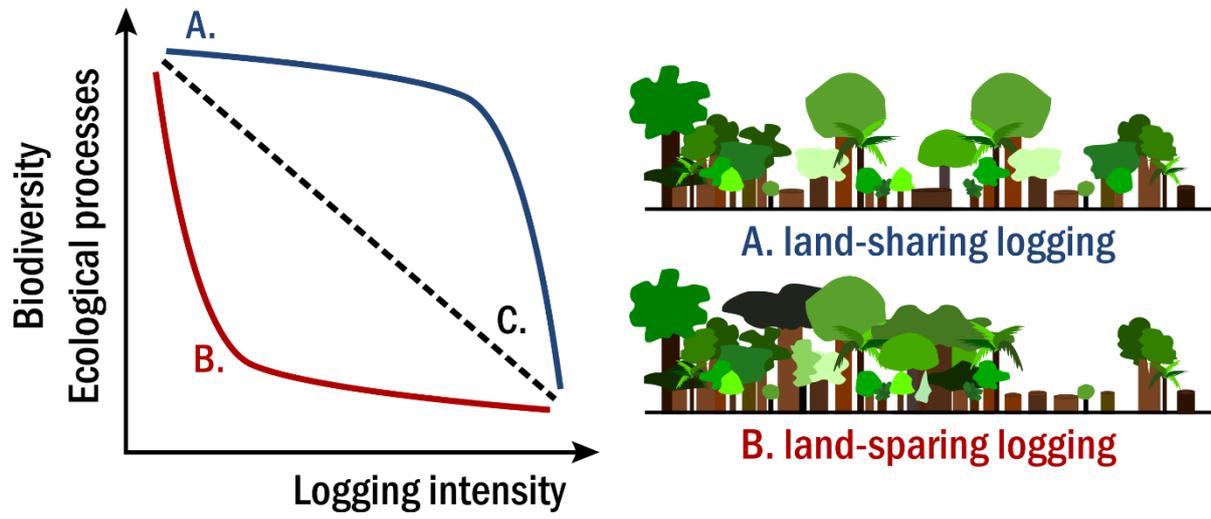
Dung beetle metrics	Model	AICc			RSS	
		Local-scale	Broad-scale	Delta AICc	Local-scale	Broad-scale
<i>Species richness</i>	NULL	211.14	211.14	0	880.74	880.74
	LINEAR	204.69	204.91	0.22	687.01	691.52
	BROKEN STICK	<b>199.82</b>	<b>202.22</b>	<b>2.4</b>	<b>561.25</b>	<b>602.32</b>
<i>Biomass</i>	NULL	176.69	176.69	0	319.79	319.79
	LINEAR	170.71	170.92	0.21	252.87	254.47
	BROKEN STICK	<b>168.66</b>	<b>169.88</b>	<b>1.22</b>	<b>224.51</b>	<b>232.7</b>
<i>Species composition</i>	NULL	-28.21	-28.21	0	0.77	0.77
	LINEAR	-32.09	-31.57	0.52	0.65	0.66
	BROKEN STICK	<b>-36.64</b>	<b>-32.16</b>	<b>4.49</b>	<b>0.54</b>	<b>0.61</b>
<i>Soil bioturbation</i>	NULL	533.84	533.84	0	11665354	11665354
	LINEAR	<b>532.91</b>	<b>529.48</b>	<b>3.42</b>	<b>10699415</b>	<b>9674984</b>
	BROKEN STICK	534.51	531.44	3.07	10574136	9661702
<i>Dung removal</i>	NULL	<b>390.34</b>	<b>390.34</b>	<b>0</b>	<b>171338.89</b>	<b>171338.9</b>
	LINEAR	392.33	392.23	0.1	171279.74	170789.2
	BROKEN STICK	392.53	394.2	1.16	162472.89	170624

681 Models: Null model (NULL), generalized linear model (LINEAR) and broken stick models  
 682 (BROKEN STICK). AICc: Akaike information criterion with small sample correction;  
 683 Minimum observed AICc are presented in bold. Delta AICc: calculation was based on the  
 684 difference between broad-scale AICc results minus local-scale values. Residual Sum of  
 685 Squares (RSS) from local- and broad-scale models represent the overall differences between  
 686 data and the values predicted by each model.

687 **Figure legends**

688 **Figure 1.** Theoretical non-linear relationships between logging intensity and metrics of  
689 ecological integrity. Concave (or concave-down) responses to increasing logging intensity (A,  
690 in blue) would support land-sharing strategies, with logging intensities set below the  
691 changepoint. Convex (or concave-up) responses (B, in red) suggest land-sparing would be a  
692 more effective way of preserving biodiversity and ecological functions. Existing evidence  
693 (Burivalova et al., 2014) suggests there is a linear decrease in species richness across multiple  
694 taxa (C).

695 **Figure 2.** Best fit models representing the responses of dung beetle species richness (a),  
696 biomass (b), species composition (c), and soil bioturbation (d) to logging intensity ( $\text{m}^3 \text{ha}^{-1}$ ) at  
697 two scales. LS shows the logging intensity measured at the sampled unit (local scale, 10 ha),  
698 while BS represents the logging intensity average within the sampled unit and its eight  
699 neighbour units (broader scale, 90 ha in total). The  $\Delta$  calculation was based on the difference  
700 between post-logging results minus pre-logging data. The black dots represent the 34 sampled  
701 units with different logging intensities. The regression lines from linear (blue) and broken-stick  
702 (red) regression models result from fitting the data to linear models and the shadow represents  
703 their 95% CI. Vertical dotted lines represent the threshold point (black line) and its 95%CI  
704 (grey lines). Non-best fit models are shown in Figure A.6 - Appendix A).

705 **Figures**

706

707 **Figure 1.**

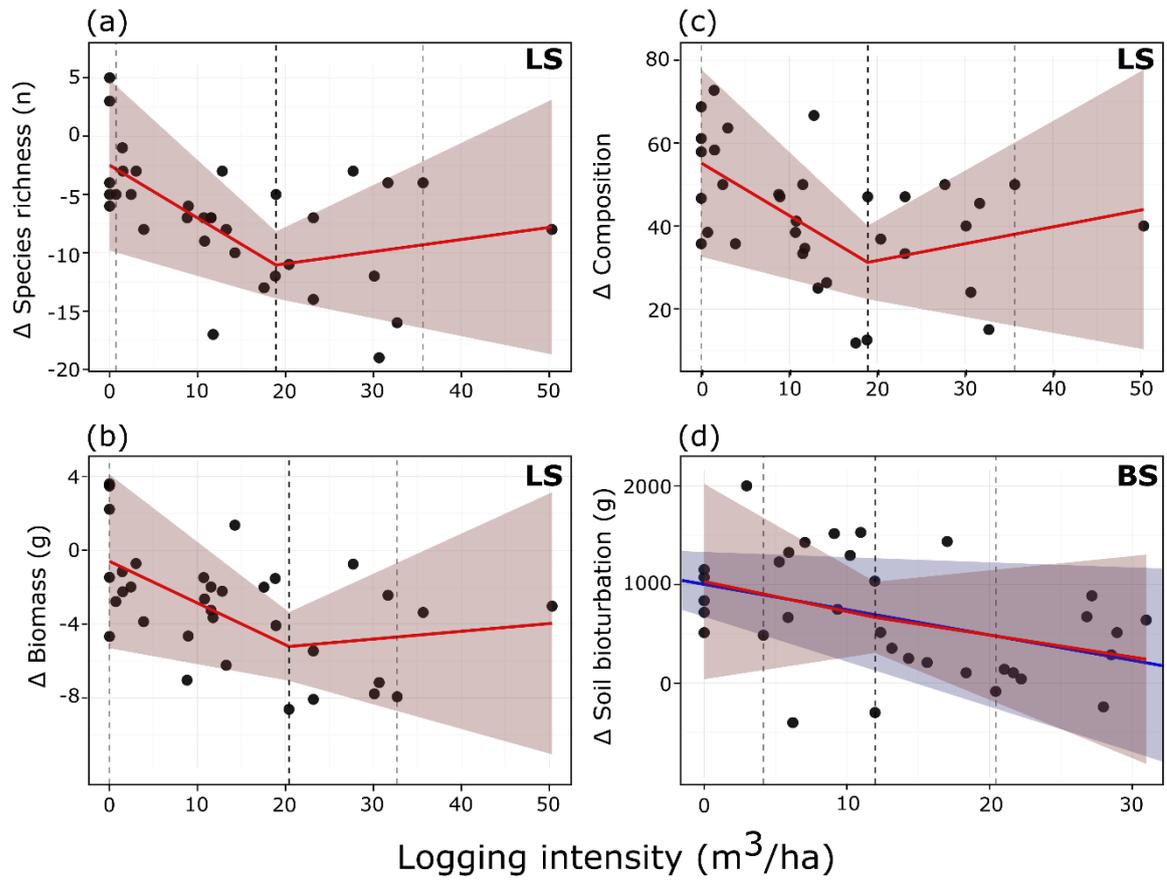


Figure 2.